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Preliminary Notes and Speculations on the *Triseriatus* Group of Rattlesnakes in México

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ABSTRACT: A new subspecies of rattlesnake, *Crotalus gloydi lautus,* is described from the states of Veracruz and Puebla, México; the type is in the U. S. National Museum, collected near El Limón Totalco, Veracruz. Brief diagnoses are given for the five subgroups of the *triseriatus* group of *Crotalus,* based upon scutellation and partly upon cranial characters. One theory of the phylogeny of the members of that group is discussed, and a possible means of reconciling the apparently opposing ideas of peripheral specialization and central specialization is suggested.

RECENT collections from México of the small rattlesnakes comprising the *triseriatus* group have revealed the existence of a previously undefined species subgroup and have made possible a clarification of the relationships of the known forms of the entire group. All the forms of the subgroup of which I am aware have been described, save for one, whose description follows.

The material which furnishes the basis for these notes has been secured partly through the efforts of the members of the Department of Fish and Game at the Agricultural and Mechanical College of Texas; and partly by Dr. E. H. Taylor and myself. I am much indebted to Dr. W. B. Davis and Mr. Max M. Whisenhunt of Texas A. and M. College, and to Doctor Taylor, for permission to study their specimens. To Doctor Taylor I owe a double debt of gratitude for his generous counsel and innumerable other courtesies.

I

Crotalus gloydi lautus subsp. nov.

Holotype. U. S. Nat. Mus. No. 110598, collected by Dyfrig McH. Forbes at the lava beds about one kilometer east of El Limón Totalco, Veracruz, on March 1, 1940. *Paratypes.* E. H. Taylor-H. M. Smith No. 5475, same locality, collected by E. H. Taylor and

H. M. Smith, August, 1932. Texas Coöperative Wildlife Collection No. 822, Lago Salado, about five kilometers west of El Limón Totalco, in the state of Puebla, 8,300 ft., July 25, 1942, collected by S. H. Wheeler.

Diagnosis. A member of the *triseriatus* group with no subloreals; postseminasal* in contact with first and second supralabials; loreal generally (?) in contact with supralabials. Pattern of 41 to 44 small, oval spots in a middorsal series; belly nearly immaculate. Differs from *transversus* in having oval blotches instead of narrow crossbands and generally (?) in having the loreal in contact with the supralabials and the lower preocular divided. Differs from *gloydi* in having a larger postseminasal in contact with two instead of just one supralabial, and generally (?) in having the lower preocular in contact with the loreal.

Description of holotype. Adult male. Rostral moderate, portion visible from above about half as long as broad; two large internasals, narrower laterally than medially, length about two-thirds width; a pair of large, oval canthals, somewhat longer than broad, separated from each other medially by a single, elongate scale nearly as large as an internasal; supraocular flat, twice as large as a canthal, slightly longer than distance from end of snout; four scales in a transverse row between supraoculars behind canthals, two (somewhat larger) in the next row, and three in a third row; scales on head posterior to supraoculars nearly uniform in size.

Naris pierced at about the middle at the lower border of nasal; latter completely divided, upper portion of anterior section projecting far posterior to the level of the lower portion; postseminasal less than half size of preseminasal, broadly in contact with first supralabial, narrowly with second, and narrowly with internasal; loreal large, rounded, in contact with second supralabial, canthal, postseminasal, upper and lower preocular, and the anterior pit scale; upper preocular single, lower divided into anterior and posterior halves; scale bordering lower edge of pit wedged between preocular and lacrimal, narrowly separated from orbit; a single row of two scales between orbit and supralabials; two postoculars (on one side the lower postocular and posterior subocular are fused); length of orbit, 3 mm., half its distance from tip of snout. (Fig. 1.)

Supralabials 9-9, posterior border of orbit above the middle of the fifth; infralabials 9-9, the first of each side in contact medially; one pair of small chinshields.

* The terms subloreal, preseminasal and postseminasal are defined on p. 82; see, also, figs. 1-4.

Dorsal scales moderately strongly keeled, except those in the outer two rows; scale rows 21-21-15; ventrals 161; caudals 25, the posterior 3 paired. Total length, 480 mm.; tail length, 40 mm.; basal rattle, 5.5x3 mm.

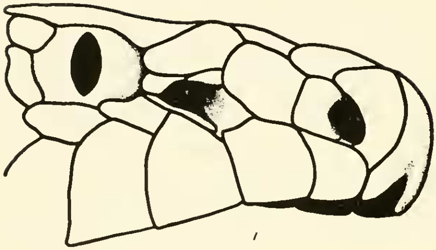
Dorsal surface pale brown, with 40 dark brown, black-edged median blotches on body, 7 on tail. The blotches are separated from each other by about 1½ scale lengths; they are nearly twice as broad as long, and cover about 2½ scale lengths longitudinally and about 6 or 7 transversely. A dorsolateral row of very indistinct, rounded spots alternates with the middorsal series, occupying the sixth and seventh scale rows. A lateral row of somewhat more distinct spots, alternating with those of the dorsolateral row (coinciding with those of the median row) occupies the 3d, 4th, and 5th rows. A sublateral row of dim spots, alternating with the preceding, occupies the 1st and 2d rows.

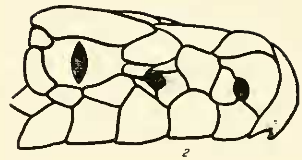
The only distinct headmarking is a dark postocular stripe disappearing a short distance back of the angle of the mouth and involving the upper portion of the supralabials; the edges of the band are well defined and straight, bordered with white below and with gray above. The top of the head is generally gray brown between the postocular stripes, varied only by a pair of dim darker spots in the anterior parietal region just back of the supraoculars. The snout, including the anterior supralabials, is dark gray, but the color fades below the eye so that the posterior supralabials are white except for the upper edges. The entire ventral surface of the head is very dark, and darkest on the chin.

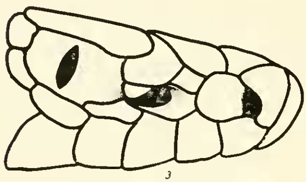
Belly nearly white, with scattered dark stippling concentrated laterally. Subcaudal surface moderately darkly stippled.

Variation. In No. 5475, several of the small dorsal head scales are fused between and in front of the level of the orbits (Fig. 2). The lower preocular is divided as in the type, and the loreal bears much the same relation to other scales, except that it is in contact with the upper posterior border of the preseminasal, separating the postseminasal from contact with dorsal scales. The suboculars are in a single row as in the type, and the labials are the same. It is a young male, measuring 218 mm. snout to vent, the tail, 18 mm.; ventrals, 161; caudals, 24. Blotches as in type, 44 on body, 6 on tail.

No. 822 seems somewhat aberrant in certain respects. Two juxtaposed scales intervene medially between the canthals. The lower preocular is single, tapering anteriorly, and on one side is narrowly in contact with the loreal *inside* the pit (Fig 3): on the other side the scales are narrowly separated (Fig. 4).







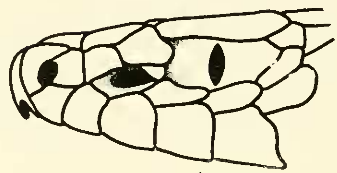


FIG. 1. Lateral view of orbitonasal region of head of *C. g. lautus*. From USNM 110598, type.
FIG. 2. As in Fig. 1, from EHT-HMS 5475, paratype.
FIG. 3. As in Fig. 1, from TCWC 822, paratype, right side.
FIG. 4. As in Fig. 3, left side.

The loreal is greatly reduced on one side, where the postseminasal is greatly enlarged; on that side the pit scale contacts the nasal below the loreal, and the postseminasal contacts the canthal and internasal and is nearly as large as the preseminasal. On the other side the loreal is only slightly reduced, narrowly contacting the labials, but the postseminasal remains in contact with both canthal and internasal. The suboculars and labials are as in the type except 8 infralabials occur on one side. The specimen is a young female measuring 255 mm. snout to vent, the tail, 20 mm.; ventrals, 153; caudals, 20.

II

SUBGROUP COMPARISONS

Gloyd's recent monograph on *Crotalus* (Special Publ. Chicago Acad. Sci., No. 4, 1940, pp. i-viii, 1-270, pls. 1-31, maps 1-22, figs. 1-10) recognizes 7 forms in the 2 species of the *triseriatus* group, 5 belonging to *triseriatus*, and 2 to *lepidus*. The forms now known are as follows:

OMILTEMANUS SUBGROUP:

Crotalus omiltemanus Günther.
Crotalus gloydi gloydi Taylor.
Crotalus gloydi lautus subsp. nov.
Crotalus transversus Taylor.

PRICEI SUBGROUP:

Crotalus pricei miquihuanus Gloyd.

Crotalus pricei pricei Van Denburgh.

TRISERIATUS SUBGROUP:

Crotalus triseriatus anahuacus Gloyd.

Crotalus triseriatus triseriatus (Wagler).

LEPIDUS SUBGROUP:

Crotalus lepidus klauberi Gloyd.

Crotalus lepidus lepidus Kennicott.

SEMICORNUTUS SUBGROUP:

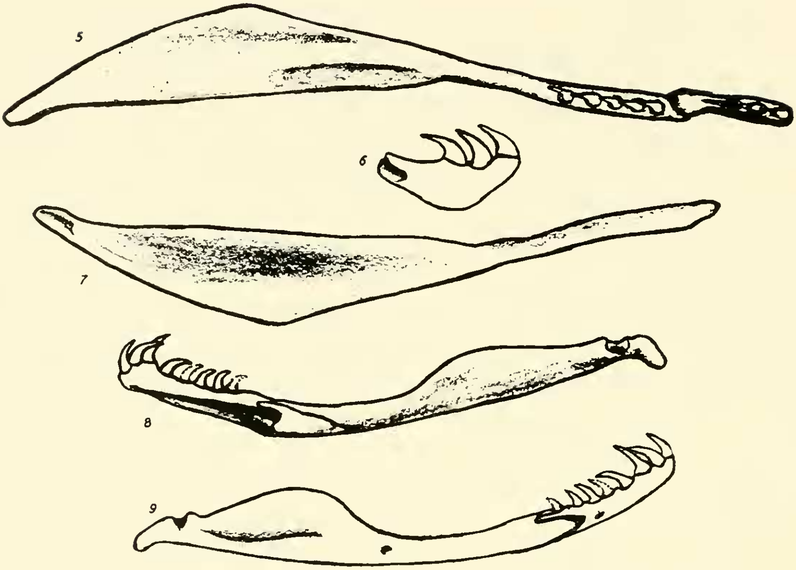
Crotalus semicornutus Taylor.

OMILTEMANUS SUBGROUP

The new subgroup mentioned previously is that here referred to as the *omiltemanus* subgroup. Its segregation as a group of forms distinct from the rest of the *triseriatus* group is of considerable importance. Heretofore its members (except for *transversus*) have been treated as subspecies of *triseriatus*. Certainly that disposition is incorrect, but the arrangement of the forms within the subgroup—as races of a single species or involving several species—is not yet clear.

Primary characteristics. The forms are distinguished from *triseriatus*, whose geographic range they overlap, by a number of striking features. Of greatest importance are the relationships to each other of the scales on the sides of the head; until recently the importance of certain of these scales has not been fully appreciated. In all members* of this section the subloreals are completely lacking (Figs. 1-4, 18); they are present (1 to 3) in all other species of the genus (Figs. 15-17). The scales referred to as subloreals are small ones interposed between the loreal and labials, and between the nasal and the pit scales. Since the term loreal has been restricted by Klauber (Trans. San Diego Soc. Nat. Hist., vol. 8, 1936, p. 222) to apply in rattlesnakes to "the scales [one or more] on the side of the head between the postnasal and the preocular . . .." and is generally used in this sense by other specialists, the scales described above cannot be considered as lower loreals; upper and lower loreals do occur in rattlesnakes, but both are between the "postnasal" and the preocular. Thus in the absence of any other term in general use I suggest "subloreal" as one sufficiently appropriate.

* In the type of *transversus*, according to the drawing (Taylor, Univ. Kan. Sci. Bull., vol. 30, 1944, fig. 10, p. 48), there appears to be a subloreal on one side. The scale is, however, a pit scale.



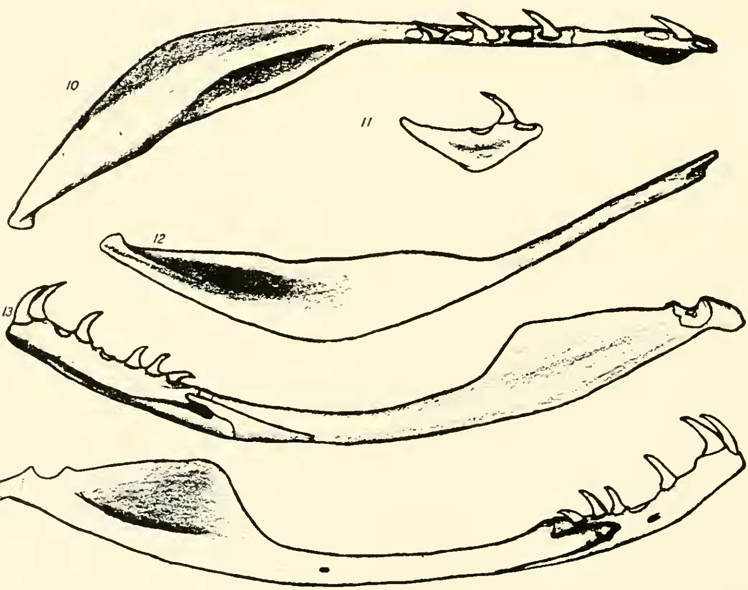


FIG. 5. Ventral view of right palatine and pterygoid of *C. g. lautus*. From USNM 110598, type.
FIG. 6. As in Fig. 5, lateral view of right palatine.
FIG. 7. As in Fig. 5, dorsal view of right pterygoid.
FIG. 8. As in Fig. 5, medial view of right lower mandible.
FIG. 9. As in Fig. 5, lateral view of right lower mandible.

FIG. 10. Ventral view of right palatine and pterygoid of *C. t. triseriatus*. From EHT-HMS 21502, from Tacícuaro, Michoacán (*var. pallidus*).
FIG. 11. As in Fig. 10, lateral view of right palatine.
FIG. 12. As in Fig. 10, dorsal view of right pterygoid.
FIG. 13. As in Fig 10, medial view of right lower mandible.
FIG. 14. As in Fig. 10, lateral view of right lower mandible.

There is an indication that at least one skeletal character may be correlated with the *omiltemanus* section, but since I have been able to check it only in *lautus*, no generalizations are advisable. One pterygoid bone examined of *lautus* bears 5 teeth (Fig. 5); on the other hand each of the 2 pterygoids of *pricei* and 6 of *t. triseriatus* bears 6 or 7 teeth (Fig. 10). Since the head is notably shorter in species of the *omiltemanus* subgroup than in other species (except perhaps *pricei*) the lesser tooth number is not surprising. Other differences, some very striking, occur in shapes and contours of the palatines, pterygoids and dentaries of the 3 forms examined, but their significance is not clear. The palatine, for instance, is very short in *lautus*, more elongate in *triseriatus*. In *lautus* the posterior end of the pterygoid lacks the peculiar, ridgelike process on the dorsal surface that is present in *triseriatus;* also the concavity on the dorsal surface is more central in position. In *lautus* the palatine articulates on the medial side of the anterior tip of the pterygoid, while in *triseriatus* the suture between the two appears (in ventral view) to be transverse. One of the characters believed to be most significant is the direction taken by the anterior border of the splenial ventral to the anterior meckelian foramen; in *triseriatus* it passes a considerable distance posteriorly, while in *lautus* it passes almost straight ventrally from the posterior border of the foramen. The flared dorsal border occupying the posterior third of the length of the dentary is more accentuated in *triseriatus* than in *lautus*. The depth of the angular notch in the dentary (as seen in lateral view), and the positions of the two lateral foramina, also differ. Other differences, which may be of considerable significance, can be discerned by making comparisons of the accompanying figures (Figs. 5-14).

Secondary characteristics. But little less significant than and almost if not quite as useful as the characteristics mentioned above are a number of others which find few exceptions. The supralabials are with rare exception 9; that number occurs elsewhere only in *pricei*, of the *triseriatus* group. The supralabial below the posterior border of the orbit is the 5th (Figs. 1-4, 18), while in all others of the group (Figs. 15-16), except *pricei* (Fig. 17), it is the 6th or 7th.

Of great interest in the entire group is the conformation of the nasal. This scale is always split (perhaps rare exceptions) in rattlesnakes, and perhaps for this reason has generally been treated as two separate scales—postnasal and prenasal. These terms, however, are in general use in other groups of reptiles for scales following or preceding, respectively, the nasal, which may or may not be split. The concept of the nasal is a scale in which the nasal opening is pierced; a vertical suture may split the scale into anterior and posterior halves, but these are still parts of the nasal, and are not prenasals or postnasals in the sense of being scales preceding or following the nasal itself. It is the usual procedure to refer to th parts of the divided nasal as the anterior or posterior section, but since this is clumsy and involves quite a few words the terms *preseminasal* and *postseminasal* are suggested.

In the *omiltemanus* subgroup, the postseminasal is always in contact with the first or first and second supralabials (Figs. 1-4, 18); this condition is found elsewhere in the group only in *pricei* (Fig. 17) and in rare *t. triseriatus* (Fig 15). and in none of even these is there contact with the second supralabial. It follows, and is true, that in the four forms of the *omiltemanus* subgroup (Figs. 1-4, 18);

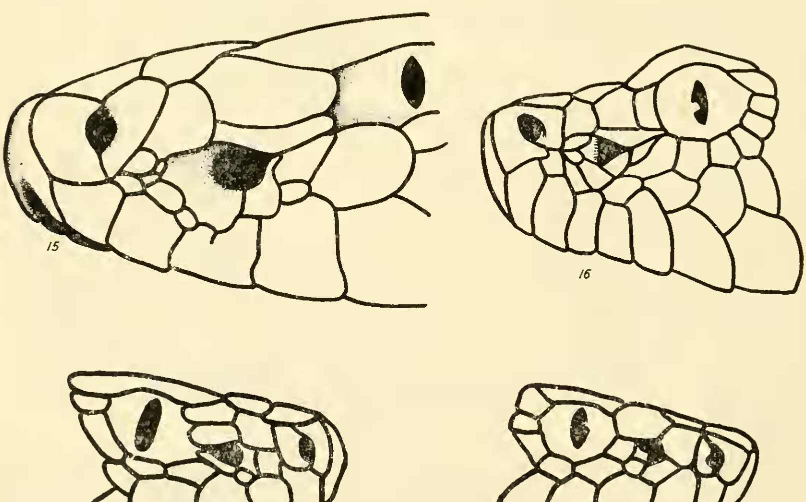


FIG. 15. Lateral view of orbitonasal region of head of *C. t. triseriatus*. From USNM 46465, Ameca, Jalisco.
FIG. 16. As in Fig. 15, *C. l. klauberi*. After Stejneger.
FIG. 17. As in Fig. 17, *C. p. miquihuanus*. After Gloyd.
FIG. 18. As in Fig. 18, *C. omiltemanus*. After Gloyd.

the lower border of the preseminasal is not produced posteriorly, while in *triseriatus* and *lepidus* (all forms of each) it is markedly produced posteriorly (Figs. 15, 16).

The dorsal border of the postseminasal may be in contact with the canthal and internasal, internasal only, or neither scale in the various forms of the *omiltemanus* subgroup (Figs. 1-4, 18); no one condition is necessarily constant for any one form. In *pricei* (Fig. 17), however, the dorsal border of the postseminasal is always (so far as known) in contact only with the internasal, while in *triseriatus* and *lepidus* (all forms of each) generally both canthal and internasal are contacted. Therefore the loreal may be in contact with both canthal and internasal, or with the canthal only, depending upon the nature of the nasal.

The loreal may in the *omiltemanus* subgroup be in contact with the labials, or it may be separated (Figs. 1-4, 18); in the latter case the separation is always by means of contact of the nasal and pit scales, never by subloreals.

Klauber (*loc. cit.*) states that a loreal is always present in rattlesnakes. Taylor (Univ. Kan. Sci. Bull., vol. 30, 1944, pp. 47-48, fig. 1) however, says the loreal is absent in *transversus,* and accounts for the extra scale by assuming it to be an anterior section of a divided upper preocular. Other specimens that have become available since Taylor made his study, however, show intermediate conditions that indicate rather conclusively that the scale in *transversus* is actually a loreal, not a part of a preocular.

The lower preocular is generally separated from the loreal, or split into two scales, in members of this section (not evident in figures). Only in *transversus* is the scale entire and in contact with the loreal. In all other sections of the group the scale contacts the loreal, and is very rarely divided (I have seen it divided in but one, a *t. triseriatus*).

A further characteristic is the reduced dorsal scale rows of the *omiltemanus* subgroup. All specimens have 21-17 (15) rows. In *pricei* the rows are usually 21 at the middle of the body, but in all others of the group 23 rows is the usual number.

Finally the body size is smaller, in general, in the *omiltemanus* subgroup; the head is likewise proportionately smaller, and the rattle smaller. In view of the characteristics cited there can be no question, I think, of the distinctness of the *omiltemanus* subgroup apart from the others of the *triseriatus* group. But as stated before the relationship to each other of the various forms in that section is not yet completely clear.

Status of forms. The form *omiltemanus* is one of the best differentiated of its subgroup, because of the high ventral count. No overlapping between its ventral counts (172 to 183) and those of other members of the subgroup (145 to 161) is apparent, and moreover only *klauberi,* of all other forms of the entire group, overlaps the counts of *omiltemanus* to any extent whatever (152-175). That character should then be given considerable weight, and because of it I regard *omiltemanus* as a species instead of a subspecies. The number of dorsal blotches (51 to 60) is also unique among members of the *omiltemanus* subgroup (others with 34 to 45); *anahuacus* and *pricei* (both forms), however, overlap this range completely. Moreover the character of the lower preocular is not absolutely unique (separated from loreal), as one specimen of *lautus* has been examined with a similar condition on one side, and the type of *gloydi* also has the scales separated.

Nevertheless the total characteristics of *omiltemanus* favor its consideration as a full species. Since there is some degree of continuity of ecological conditions (Fig. 20) between the areas occupied by *omiltemanus* and *gloydi,* however, the possibility of intergradation is not to be overlooked.

The remaining forms of the section comprise a compact unit of very uniform character. They are from distinct geographical areas: *gloydi* from Oaxaca, *transversus* from the Morelos-Mexico border, and *lautus* from the central Veracruz-Puebla border (see map, Fig. 20). The latter is known from 3 specimens, *transversus* from two, *gloydi* from one. The character of the loreal and postseminasal are generally to be considered of considerable importance in distinguishing the forms of the group, and in the present three some widely divergent types occur. In *gloydi* the postseminasal is greatly reduced and in contact with only the loreal, first labial and preseminasal, while in *transversus* it is the loreal that is greatly reduced, resulting in contacts of the postseminasal with the canthal, internasal, loreal, pit scale, first and second labials, and preseminasal. Two specimens of *lautus* from the border area of Veracruz and Puebla near Perote are rather like *gloydi* in this character, except that the postseminasal is a little larger and contacts the second labial and, in one specimen, the internasal. But a third specimen from the same area is exactly like *transversus* on one side of the head (Fig. 3), and approaches that condition on the other (Fig. 4). It cannot now be assumed that the latter specimen is of a different species than the other two specimens from the same area, and thus one is forced to regard the nature of the loreal and postseminasal with suspicion in this subgroup until enough specimens are available to show the normal range of variation. The scales may be of great importance and of considerable constancy in other members of the group, yet in this subgroup some variation must be anticipated.

The form *gloydi* is distinguished from *lautus* and *transversus*, then, on the basis of the great reduction of the nasal (questionable), the separation of lower preocular and loreal (not infallible, also known on one side of some specimens of *lautus*), and upon the pattern (very similar to that of *lautus*). The type (which I have examined) has about 42 blotches on the body, and these are more or less quadrangular or oval in outline, covering 2 to 3 scale lengths and occupying 5 to 7 scale rows; they are separated from each by about one scale length. There is nothing in these characters to encourage regarding *gloydi* as a species distinct from *lautus*.

C. *transversus* has a mottled belly, and very narrow crossbands or spots 34 to 45 in number, which are split or almost divided on the middorsal line. Known specimens also have the postseminasal in contact with the pit scales, and the preocular in contact with the loreal; but one *lautus* specimen shows the same condition, in each category, on one side of the head. To this species I believe should be referred Martín del Campo's specimen (Anal. Inst. Biol., vol. 11, 1940, pp. 472-473, fig.) from Cempoala, Morelos. The form is more distinct from the other two than the latter are from each other, but only in pattern; and that pattern, particularly as exemplified by Martín del Campo's specimen, is not so remotely different from that of *lautus* that intergradation is not easily conceivable. Yet for the present, the greater degree of difference of *transversus* from *lautus* and *gloydi* leads me to regard the former a distinct species.

C. g. lautus has oval blotches, longer than in *transversus*, not interrupted at the middorsal line, and the belly is marked only with fine, scattered dark stippling. The postseminasal is reduced but in contact with 2 labials, and may or may not be in contact with the pit scales and with the internasal alone or both the internasal and the canthal. The relationship with *gloydi* appears to be very close and that with *transversus* is scarcely less so.

PRICEI SUBGROUP

The two forms of this species are associated together on the basis of morphological and patterns similarity, and geographic probability. Each has a single subloreal (Fig. 17), contrary to the *omil-*

temanus subgroup which has none (Figs. 1-4, 18), and the other subgroups which normally have several. The supralabials are usually nine, and the fifth lies below the posterior border of the orbit, as in the *omiltemanus* subgroup, and thus the species is a rather short-headed one. Of great significance is the fact that the preseminasal is not produced at its ventral border, but is in contact with only about the anterior half of the upper surface of the first supralabial (Fig. 17); in *triseriatus, lepidus* and *semicornutus* the border is so prominently produced posteriorly that it nearly or quite reaches the second supralabial, generally (Fig. 16) separating the postseminasal from the labials (not always, Fig. 15). Likewise in *pricei* the postseminasal is in contact above only with the internasal, while in *triseriatus* and *lepidus* the scale generally touches both canthal and internasal. The scale rows are generally twenty-one medially in *pricei,* twenty-three in *triseriatus* and *lepidus.* These are the chief characteristics by which the two forms differ from others; and there can be no question that together they comprise a distinct species. The species finds its closest relatives at least so far as external characters are concerned, not in *triseriatus* but in the *omiltemanus* subgroup. *C. transversus* approaches it most closely in pattern. The characters of the pterygoid, palatine and lower jaw bones, however, approach or duplicate those of *triseriatus.*

TRISERIATUS SUBGROUP

The preceding discussion has brought out differences between *triseriatus, pricei,* and the *omiltemanus* subgroups. The chief features mentioned that define *triseriatus* as a species are the numerous (10 or more) supralabials; 6th, 7th and 8th labial below posterior border of orbit (Figs. 15, 16); several (rarely one) subloreals (Figs. 15, 16); postseminasal generally in contact with canthal and internasal (Fig. 15); preseminasal produced posteriorly (Fig. 16); 23 or 25 scale rows at middle of body. In addition the dorsal blotches on the body are not less than 25. The species is completely and well differentiated from others of its group.

The two forms of the species are rather clearly subspecies, as their characters overlap and they occupy adjacent ranges. The chief differences between *t. triseriatus* and *t. anahuacus* are in number and size of dorsal blotches, and in number of ventrals. The latter has more numerous oval blotches (usually 40 or more, *triseriatus* with usually less than 40 quadrate blotches) and fewer ventrals. Specimens now referred to *t. triseriatus,* however, may represent still other forms not now clearly distinguishable.

The closest relatives of *triseriatus* are not in the previously considered forms, but in *lepidus*. There is a great similarity between the two species, and I believe it indicates relatively close relationship. The frequent occurrence of a divided upper preocular in *triseriatus* links it with *lepidus,* as does the curious form of the nasal, the several subloreals, the numerous supralabials, and the numerous scale rows. Klauber (Copeia, 1940, No. 3, pp. 206-207) refers to differences in hemipenial structure, but in external features, the two species are so alike that one specimen from Santa Teresa, Nayarit (U. S. Nat. Mus. No. 46333) is the subject of some disagreement as to which species it represents. Gloyd (*op. cit.,* p. 87) places it in *t. triseriatus,* while I would call it a *l. klauberi.* It has only 22 cross-bands on the body (including the occipital band), and although these are narrow (occupying only 5 to 8 scale rows) except near the tail, they are spaced and shaped as in *lepidus,* and are serrate-edged as in that species. Since the known minimum in *triseriatus* is 25 body blotches, while the range in *lepidus* is 14 to 23, the specimen falls best in *lepidus,* whose pattern it matches in other respects. It resembles *triseriatus,* however, in the gray-brown ground color, the very dark belly and chin, and the absence of a division in the upper preocular. Since apparently all other *lepidus* invariably have the upper preocular divided, this exception is extraordinary. Unfortunately the specimen is a female, so no comparisons of hemipenes are possible. In view of the variability of the head scales, I prefer to follow the indication of the pattern in allocating the specimen to *lepidus.* It does not, however, agree completely with the form of *lepidus* (*klauberi*) known from the same general area, for it has a dark postocular stripe and a darkly mottled belly (no stripe, belly nearly or quite immaculate in *klauberi*). Altogether the specimen appears quite intermediate in character between *triseriatus* and *klauberi*; it may represent a distinct race or species, or, of course, a hybrid. Further specimens will be necessary to arrive at a definite conclusion. In any event the postulate of a close relationship between *lepidus* and *triseriatus* is given strong support by the specimen.

SEMICORNUTUS SUBGROUP

This recently described form is almost as much of a puzzle as the preceding specimen from Nayarit. The single known example is unique in the development of the supraocular, but in most other respects is very similar to *lepidus.* The blotches resemble those of the other species of the *triseriatus* group rather strongly, as they are about equally as long as broad. The species evidently demonstrates a pattern that may be close to the ancestral type of *lepidus*, for it is clear that the latter form must have been derived from something with blotches not unlike those of *triseriatus*.

III

Zoögeography and Evolutionary Discussion

The arrangement of pattern types in the *triseriatus* group suggests that *semicornutus* is the most primitive of all forms of the group in pattern. It is not, it would seem, primitive in scutellation, but is rather the most highly modified of the group. The situation requires explanation.

Migration waves. As has long been urged by many zoögeographers, and as reëmphasized by Schmidt (Amer. Midl. Nat., vol. 30, 1943, pp. 241-253), in the course of evolution of animals upon the American continents a succession of waves of more and more advanced forms radiated outward from a center of distribution in the north. Thus an aggregation of primitive forms at, for instance, the southern edge of the Mexican plateau, is not to be interpreted as indication that the edge of the plateau is a center of distribution; rather it indicates the extreme periphery of distribution of the several groups represented. The *triseriatus* group appears to fit this distributional law. The most primitive forms (*omiltemanus* subgroup) are at the extreme periphery of the range of the group (Fig. 19); they together can be visualized as the present-day counterparts of the primary portion of the first wave (IA of Fig. 21) of migration from some northern center of dispersal. As a secondary portion (IB of Fig. 21) of the first wave, the *pricei* subgroup followed the *omiltemanus* subgroup, but because of close relationship, as a member of the same wave movement, never over-ran the primary portion. Some time elapsed before a second wave, carrying along as its primary portion (IIA of Fig. 21) the *triseriatus* subgroup, migrated southward, eliminating most evidence of the first wave except in the Oaxaca and Guerrero regions, which may by that time have become inaccessible. The secondary portion of the second wave (IIB of Fig. 21) carried *lepidus* in its wake, and perhaps a tertiary portion (IIC of Fig. 21) carried *semicornutus*. Thus the picture of waves of migration might be represented as in figure 22. The number of waves, their relative importance and their temporal distinctness are purely a matter of conjecture and may well be in

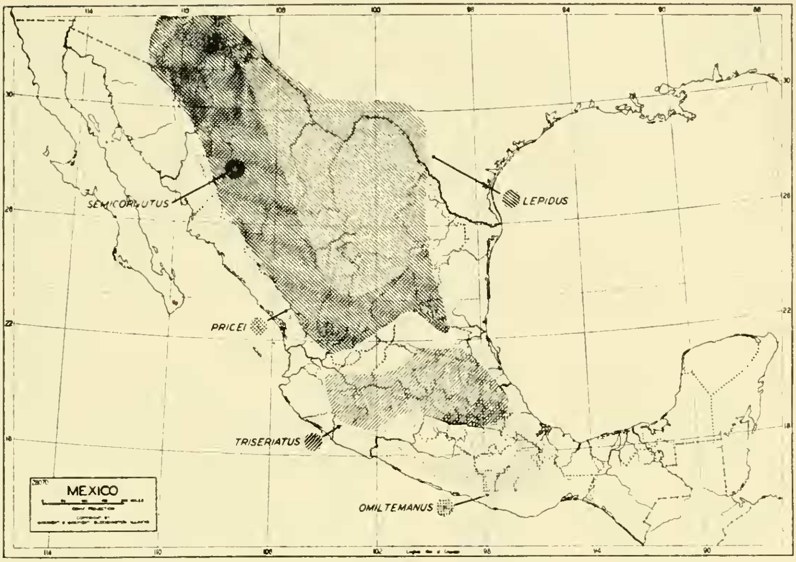


FIG. 19. Distribution in Mexico of the five subgroups of the *triseriatus* group.

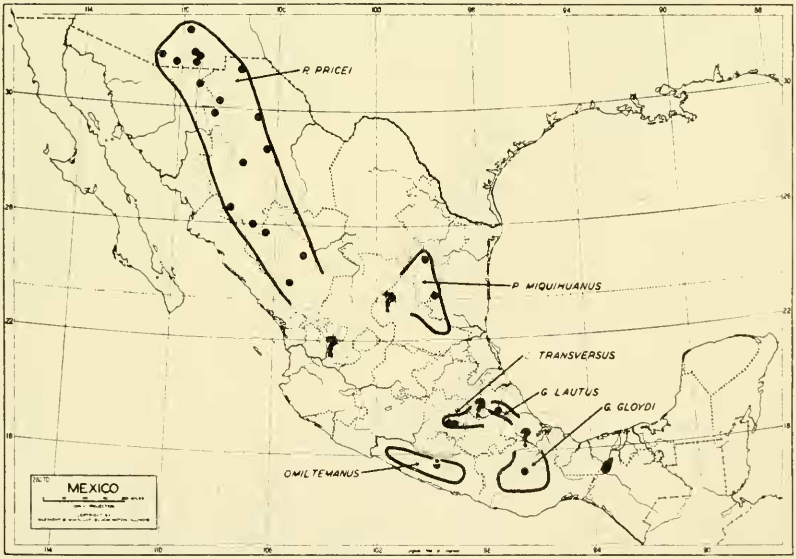


FIG. 20. Distribution of the members of the two primitive subgroups (*pricei* and *omiltemanus*) of the *triseriatus* group.

error. The succession is, however, fairly well established and it is only this that can at present be considered of significance.

Orthoevolution in scutellation. In each successive wave and wavelet of this migration an increasing modification of head scales and general external character is clearly evident. The members of the first wave (IA) are the least modified beyond a typical snake condition, while the member of the last wave (IIC) is the most highly modified of all. This is a trend which may be described as orthoevolutionary, for the modifications of each successive wave have been along the same lines almost without exception. The term orthoevolution is not used here as an explanation of the phenomenon but simply as a brief way of referring to the character of evolution in these particular features—a single-line evolution rather than a haphazard one. To what the phenomenon is due—whether selective mutation (orthogenesis) or selective elimination (orthoselection) —is not for speculation here. There is a suggestion, however, that regardless of the means, environment plays an important role in it.

The existence of an orthoevolutionary trend such as is evident in the scutellation of the *triseriatus* group cannot be explained as something inherent in the germ plasm of the group. Were that the case the oldest forms, of wave IA, would be the most highly modified of all. Clearly the modification must be dependent upon the geographic center of origin of the group. Thus the longer the animals remain in that center, the greater their modification along the specified line; and the sooner they leave, the less the modification will be. This statement agrees perfectly with the idea of waves of outward migration; members of wave IA, having left the center of origin earliest, were least changed, while that of the last wave (IIC) to leave that center was the most changed. Thus it is apparent that in this orthogenetic trend the most important factor is the existence of the animal *in a certain geographical area* in which the changes are being produced; outside of it the changes, at least in that direction, cease.

Pattern orthoevolution. There is a second orthoevolutionary trend, and that is in pattern. It is not so well defined as the trend in scutellation, but clearly exists. The members of wave I have relatively numerous and small blotches, with extremes in *omiltemanus, transversus* and *pricei*. The members of wave IIA have relatively fewer, but *anahuacus* closely parallels some members of wave IA. The forms of wave IIB have still fewer, and that of IIC least of all. The trend exists, but the direction of the trend—

whether from a primitive pattern with few blotches or one with many—is not immediately obvious. If the procedure in this case is like that in regard to scutellation, then the least modification occurs in the peripheral forms, the greatest in the most central.

But, I believe, the procedure has not been the same in pattern as in scutellation. If what is primitive in pattern were generally known, as is the primitive scutellation, there would be no doubt of

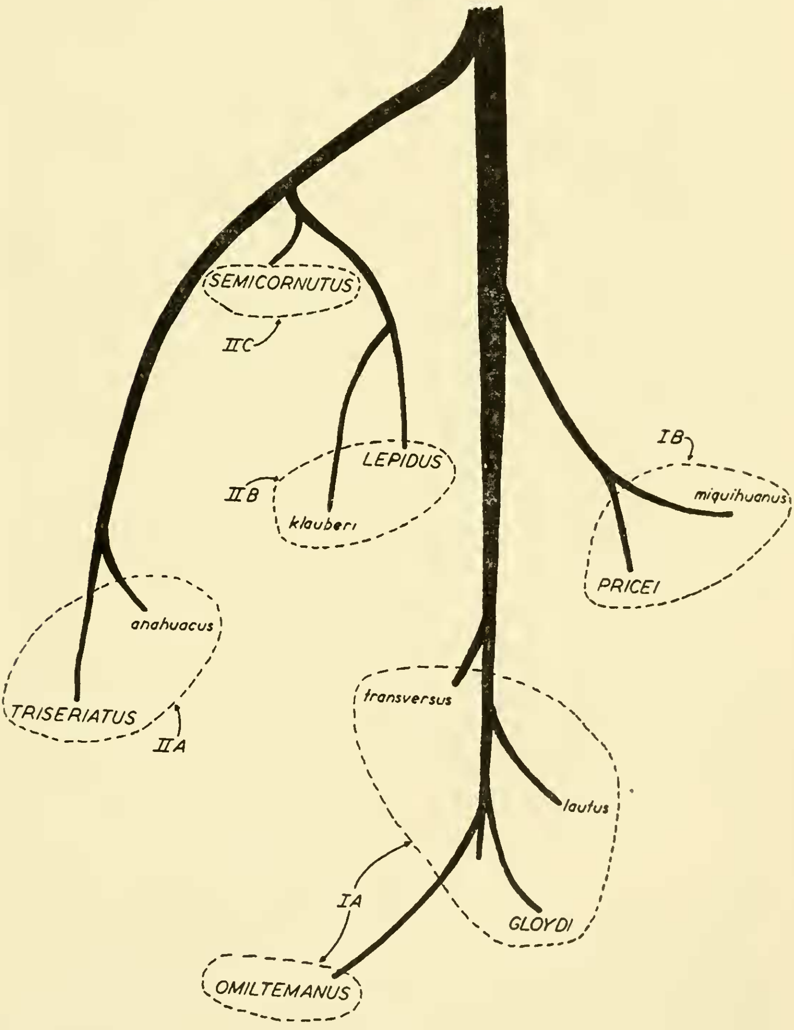


FIG. 21. Possible phylogeny of the forms of the *triseriatus* group.

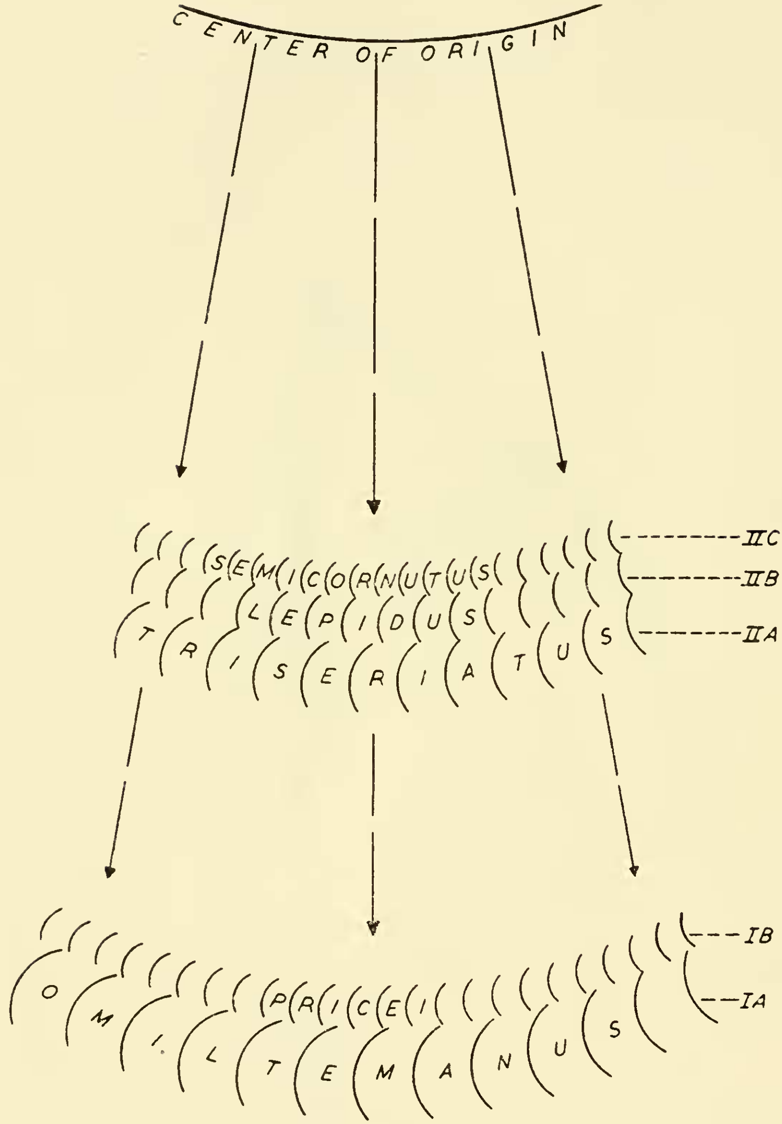


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FIG. 22. Diagram of migration waves in the *triseriatus* group.

the direction of the trend. Herpetologists have not generally agreed, however, upon the type of pattern that is primitive for snakes in general or for rattlesnake ancestors. In the absence of such knowledge we must try to determine what is primitive in the present case.

Three lines of evidence point toward the condition of few blotches as primitive.

First, there is little difference between some members of wave IIA and some of wave IA. *T. anahuacus,* for instance, is strikingly similar to *lautus* and *gloydi.* Yet waves I and II are strikingly different in scutellation. If the change was going on only in the center of origin (as in the case of scutellation) there would have been difference between the various waves equally as great in pattern as in scutellation. That there is not suggests that pattern changes occurred *after* migration away from the center of origin, although at different rates in the different waves. In such case it is reasonable to assume that the changes may continue at a more or less constant rate outside of the center of origin, and that the accumulation of change will be greatest in the forms which have been longest away from that center. By this line of evidence a primitive pattern of few blotches is suggested.

A second line of evidence is the lack of constancy of pattern within the members of one wave. In the *omiltemanus* subgroup, for instance, there is a rather considerable range of variation from almost the maximum number of blotches known in the group to a median number of some 34. Since these are all derived from one common wave-stock, it is clear that these changes in pattern occurred *after* migration to their present geographic zone. We know then that pattern evolution is not *limited* to the center of origin, and that it has progressed to a considerable degree outside of that area. Thus one is led to the same line of reasoning that was followed in discussion of the first point above.

Finally, those monographs which have dealt with the problem of pattern evolution in snakes have indicated that the trend, in blotched colubrids at least (from which the vipers presumably were derived) the primitive pattern is one of few, small blotches. The pigmented area tends to increase, either by increase in number or in size of the blotches. Increase in number may result only in a shattering and reduction in size of the spots (as in *pricei*), to preserve a certain constant of nonpigmented area (seemingly a very important factor in pattern evolution). On the other hand, it may result in a crowding and a *sudden* reduction in number of blotches by elimination of alternate marks. A second increase may follow, and then another sudden decrease in the same fashion, and so on. The blotches may expand laterally into rings instead of, or as well as, increasing in number. Should increase in *size* of the blotches be the direction of pigment expansion, instead of increase in number, then a longitudinal fusion and shattering may result, suddenly producing a striped pattern, which then goes through its own line of evolution. That all colubrids have followed this line of blotch evolution does not necessarily follow; that of *Coluber* and *Masticophis* is not readily comparable. But at least there is a parallel phenomenon in some Colubrids and in the *triseriatus* group; and that the parallelism may be of profound nature is a tempting speculation.

Positive and negative orthoevolution. If it be granted that the primitive pattern, for the *triseriatus* group, is one with few, small blotches, then it may be seen that the orthoevolutionary trend in pattern is the *reverse* of that in scutellation, for the earliest wave has the greatest instead of the least change, and the latest wave has the least instead of the greatest change.

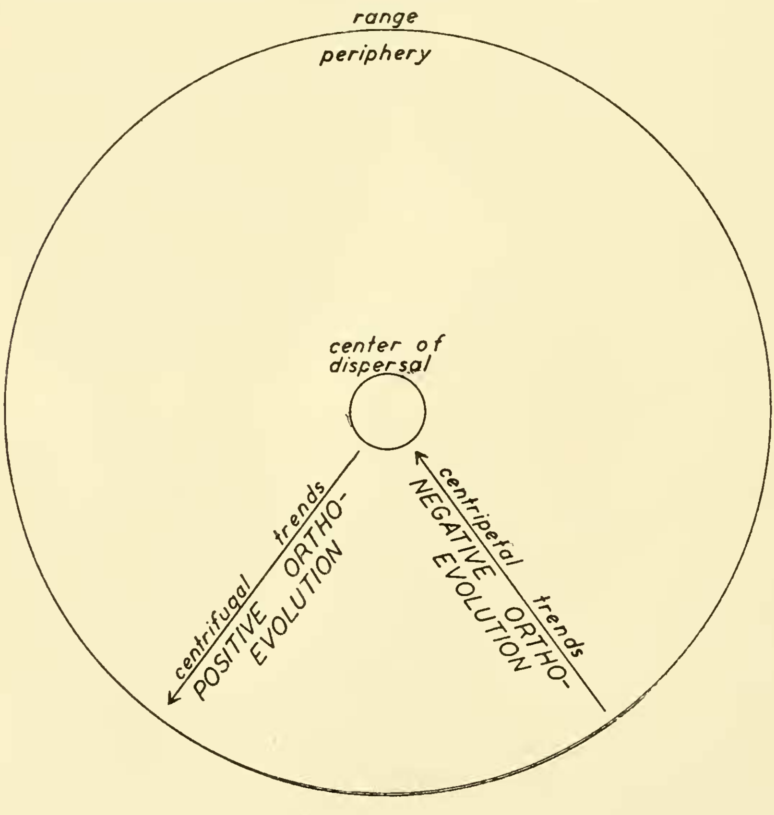

FIG. 23. Diagrammatic representation of the concept of positive and negative orthoevolution.

Thus we are concerned in pattern and scutellation with two phenomena of diametrically opposed nature—one which might be called "positive" orthoevolution (pattern), the other "negative" orthoevolution (scutellation) (Fig. 23). Negative orthoevolution may be defined as an evolutionary trend whose manifestation is dependent upon a certain limited environmental situation; it is of relatively localized occurrence. Positive orthoevolution is conceived as an evolutionary trend whose manifestation is independent of most (not necessarily all) environmental conditions; it is of relatively general occurrence.

Environmental effects. It is clear that pattern evolution continued outside the center of origin, while scutellation evolution did not. Pattern change did not occur at all times, *both* within and without the center of evolution, else all forms would be more or less alike. Given that the most primitive pattern occurs in or near the center of origin, it follows that pattern evolution occurred only or for the most part, *outside* the center of origin.

We conclude then that under the conditions existing over many thousands of years in the center of origin of the *triseriatus* group, and *only* within that area, a constant series of mutations occurred and were preserved to produce a steady orthoevolutionary trend in scutellation changes. In that area no pattern changes occurred. However, as the populations carrying these characters spread beyond the limits of this center of origin, the mutations for scutellation change ceased, and in their stead appeared another orthoevolutionary trend in mutations affecting pattern. Clearly some environmental factor operated in one place that did not in another, and its role was an important one in rattlesnake evolution. The means whereby its influence was effected is not evident.

It is interesting to conjecture that the mutation rate in the rattlesnakes discussed is more or less constant at all times, and that only the nature of the mutations is influenced by the environmental factors; and likewise that positive orthoevolution concerns survivally important characters, while negative orthoevolution involves characters of no selective value.

Matthew versus Adams. The main body of evidence derived from these rattlesnakes supports Matthew's main premise in Climate and Evolution of successive waves of migration from a northern center of dispersal. But it also shows that his second premise of peripheral occurrence of primitive forms is not wholly or always true. Certainly the peripheral forms are the earliest migrants; in this respect they are the most primitive. But Matthew did not use the term "primitive" in just that sense. He meant that the peripheral forms not only were of the earliest waves of migration but also carried the most primitive *characters*. From the above discussion it is apparent that this is not always so. Whether the peripheral forms are the most primitive in all respects depends upon the nature of the orthoevolutionary trends. If they have been in the past of local character (negative orthoevolution) then there will be no or little further change as the wave migrates peripherally. But, if positive orthoevolution occurs in some character, then the forms near the center will be the most primitive in that character. Peripheral modification, with a central primitive stock, is essentially the prime thesis of Adams' theory of group evolution. These two principles—of Adams and of Matthew—have been generally regarded as diametrically and unalterably opposed to each other. In reality they operate hand in hand, neither to the exclusion of the other, as two consistent phases of species evolution.

Primitive versus early. It is evident that the earliest migrants from the center of dispersal of the *triseriatus* group are not in all respects the most primitive. They are held in that light by most investigators because they actually are primitive in certain conspicuous characters that are usually held as important. Yet in other respects the *omiltemanus* subgroup is highly modified. The association of primitive with highly specialized characters in a single form or group is commonly known in many groups of animals, yet in spite of this fact they are continually referred to as "primitive" species. In reality the modified characters may be more numerous than the primitive ones; it is only the subjective evaluation of them that can lead one to assume that more characters, or more important ones, are primitive than modified. Obviously one should refer to primitive or modified *characters*, not primitive or modified *species*. The species is the carrier of the characters; it is neither primitive nor modified, although it may be referred to as such if its characters are preponderantly or notably of one type or the other. Actually the species should be referred to as an *early* or *late migrant* or *divergent;* in that expression is conveyed the expectation of a certain proportion of primitive or modified characters.

IV

Summary

The *triseriatus* group of *Crotalus* consists of 11 forms, as known at present, belonging to 6 species and four subgroups. The most primitive subgroup includes *omiltemanus, gloydi gloydi, g. lautus,* and *transversus,* all forms at the southern periphery of the Mexican plateau. That section comprises the remnants of the first of a series of perhaps 5 successive waves of migration from a northern center of origin. The second wave, closely following the first and of next most primitive forms included what is now *p. pricei* and *p. miquihanus.* A third wave, at a considerably later date, included *t. triseriatus* and *t. anahuacus.* A fourth wave, closely following the third, included *l. lepidus* and *l. klauberi,* while a fifth wave, following closely the preceding, included *semicornutus.*

The ancestral stock remaining in the center of origin during the periods of occurrence of migration waves mutated in such a fashion as to produce an orthoevolutionary trend of scale modification; these changes ceased in any part of the stock which migrated peripherally, so that later waves had evolved farther in this respect than the earlier waves. However, as the scale mutations ceased, pattern changes were initiated and perpetuated thereafter at a more or less (not completely constant) rate, so that in this respect earlier waves evolved to a greater degree than later waves.

The course of scale evolution is considered an example of *negative orthoevolution,* defined as an evolutionary trend whose manifestation is dependent upon a certain limited environmental situation; it is of relatively localized occurrence. The course of pattern evolution is considered as an example of *positive orthoevolution,* defined as an evolutionary trend whose manifestation is independent of most (not necessarily all) environmental conditions; it is of relatively general occurrence.

Either or both types of orthoevolution may occur in the development and distribution of any group of animals; probably generally both types occur. Predominance of negative orthoevolution in the history of any given group would result in a peripheral concentration of predominantly primitive forms (Matthew's principle) while predominance of positive orthoevolution would result in peripheral concentration of predominantly "higher" forms (Adams' principle). Thus these two apparently opposing principles are, then, to be con-

sidered not as mutually exclusive ideas, but as coöperatives of equal importance in the history of animal evolution, although it may be true that Matthew's principle of negative orthoevolution is predominant in frequency of occurrence in the history of many given sets of characters (*i. e.*, species).

The primitive pattern of the *triseriatus* group is considered to consist of few, small, median dorsal blotches.

The term *subloreal* is introduced for the scales between the loreal and supralabials, and between the nasal and pit.

The two halves of the nasal are termed *seminasals,* the anterior half as the *preseminasal,* and the posterior half as the *postseminasal.*

V

KEY TO FORMS OF THE TRISERIATUS GROUPS*

1. No subloreals; loreal in contact with labials or, if separated from labials, the interposed scales are the nasal and scales entering the pit; posterior section of nasal in contact with 1 or 2 labials; scale rows 21-21-17 (15); keels scarcely evident on posterior dorsal head scales; head very small 2
   One to three subloreals intervening between loreal and labials; posterior section of nasal not in contact with labials, or only with 1st labial; scale rows usually 23 or more anteriorly or medially, seldom 15 posteriorly; keels usually distinctly more pronounced; head larger 5
2. Ventrals 172 to 183; dorsal spots small, 51 to 60; lower preocular widely separated from loreal ....*omiltemanus*
   Ventrals fewer; dorsal spots fewer; lower preocular (sometimes transversely divided) in contact with loreal or not 3
3. Nasal in contact with only 1st supralabial; postseminasal much reduced in size, ¼ or less the size of preseminasal; latter in contact with loreal above; lower preocular separated from loreal; latter in contact with 1st and 2nd supralabials. .*gloydi gloydi*
   Nasal in contact with 1st and 2nd supralabials; postseminasal large or small; preseminasal in contact or not with loreal above postseminasal; lower preocular rarely in contact with loreal; latter in contact with one or no labials; spots oval or transverse bands 4
4. Dorsal pattern consisting of small, transversely oval, median blotches; loreal generally (?) in contact with supralabials; lower preocular generally (?) divided. *gloydi lautus*
   Dorsal pattern of paired spots which may be expanded laterally into transverse bands, but which do not cross the median line; loreal separated from supralabials; lower preocular single ....*transversus*
5. Median dorsal bands or blotches less than 24 on body; upper preocular rarely not vertically divided; anterior section of nasal produced posteriorly below naris to a point beyond a line even with the posterior edge of the naris.................. 6
   Median dorsal bands or blotches more than 24 on body; upper preocular usually not vertically divided; anterior section of nasal may be produced posteriorly below naris, but does not extend so far.. 8
6. Supraocular markedly elevated; dorsal spots 17 on body, not band-like (except the extreme posterior), each 5 to 8 scale rows in width, most about as long as broad; caudals 20 in a male.................................*semicornutus*
   Supraoculars round; dorsal spots 14 to 23, all generally band-like, much broader than long when visible; caudals in males over 20; supraocular not elevated....... 7

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* Based partly on Gloyd (*op. cit.*).

7. A dark stripe from orbit to angle of mouth; a pair of separate occipital blotches; body pattern of transversely expanded dark blotches or crossbands, interspaces frequently with secondary blotches or bands but little darker than ground color.
lepidus lepidus
Dark stripe from orbit to angle of mouth obsolete or absent; occipital blotches united; body pattern of conspicuous dark brown or black crossbands, interspaces greenish gray or bluish gray with small dark flecks or indistinct gray blotches.
lepidus klauberi
8. Ventral edge of preseminasal extending as far posteriorly as dorsal, or farther; postseminasal in contact with both canthal and internasal; generally two or more subloreals; six or more supralabials to below posterior edge of orbit; pattern of median blotches, but general color sometimes very dark or very light; upper preocular sometimes split transversely; scale rows generally 23 medially....................... 10
Ventral edge of preseminasal not extending as far posteriorly as dorsal edge; postseminasal not in contact with loreal, only with internasal; generally one subloreal; five supralabials to below posterior edge of orbit; pattern of small, paired dorsal spots, sometimes fused medially; upper preocular seldom divided transversely; scale rows 21 medially 9
9. Ventrals more than 150; general coloration usually gray; dorsal spots usually separate, in pairs ....*pricei pricei*
Ventrals less than 150; general coloration predominantly brown; dorsal pairs of spots often connected medially ....*pricei miquihuanus*
10. Body pattern of relatively large, quadrangular spots 25 to 46 in number, usually less than 40 ....*triseriatus triseriatus*
Body pattern small, elliptical spots (median) 39 to 57 in number.
triseriatus anahuacus

PLATE III

PLATE 1. *Crotalus gloydi lautus.* A, paratype. EHT-HMS No. 5475. B-C type, U. S. N. M. No. 110598.

PLATE III